# Fossils and ferns in the resolution of land plant phylogeny

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# Fossils and Ferns in the Resolution of Land Plant Phylogeny

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## I. Abstract

Fifty-two taxa of living and extinct vascular plants were evaluated in an unconstrained numerical cladistic analysis using 101 morphological characters to simultaneously resolve the phylogenetic relationships of ferns sensu lato. Included in the analysis were ferns assignable to the Cladoxylales, Stauropteridales, Rhacophytales, Zygopteridales, Ophioglossales, Marattiales, Filicales, and Hydropteridales, as well as a rhyniophyte, a trimerophyte, equisetophytes, lignophytes, and the psilotophytes *Psilotum* and *Tmesipteris*. The results placed ferns and fernlike plants in three distinct clades, indicating that ferns s.l. are a polyphyletic grade group. Fern clades consist of extinct stauropterids; extinct cladoxylaleans, rhacophytaleans, and zygopteridaleans; and eusporangiates and leptosporangiates with living and extinct species. Psilotophytes occur near the base of the tree rather than nesting with the Filicales, as hypothesized by some. These results place Ophioglossales as the sister group to Marattiales plus the leptosporangiates, supporting the hypothesis that Ophioglossales represent ferns rather than progymnosperms. These analyses are a first attempt, which includes extinct plants, to develop cladistic hypotheses for the overall topology of fern phylogeny and to lay the groundwork for more detailed analyses of relationships among the homosporous leptosporangiates.

## II. Introduction

Ferns are an extremely large and diverse group of modern land plants (Tryon & Tryon, 1982; Gifford & Foster, 1989), second only to angiosperms in the number of extant species (Rothwell, 1996b). They also have a long and rich fossil record (Stewart & Rothwell, 1993; Taylor & Taylor, 1993; Rothwell, 1996a). The modern flora includes several easily distinguished major fern taxa. The homosporous groups Ophioglossales and Marattiales are eusporangiate. These ferns have relatively large sporangia that develop from several sporangial initials and produce numerous spores at maturity (Eames, 1936). A third order of homosporous ferns, the Filicales, is the most species rich of non-angiospermous vascular plant groups (Rothwell, 1996b) and is widely regarded as leptosporangiate (Gifford & Foster, 1989). Although there is a great deal of variation within the order, filicaleans typically have relatively small and thin-walled sporangia that usually develop from one or two initials (Eames, 1936; Bierhorst, 1971) and that produce smaller numbers of spores than do eusporangiate pteridophytes (Bower, 1923–1928; Eames, 1936).

The remaining living ferns consist of heterosporous leptosporangiate genera that are either amphibious (Marsileales) or floating aquatics (Salviniales; Gifford & Foster, 1989). These genera recently have been recognized as a monophyletic group, the Hydropteridales (Hasebe et al., 1994, 1995; Rothwell & Stockey, 1994; Pryer et al., 1995; Stevenson & Loconte, 1996).

Paleontological studies document the occurrence of ferns s.l. in deposits that range from the Lower/Middle Devonian boundary to the recent (Gensel & Andrews, 1984; Galtier & Scott, 1985) and reveal that there has been a great deal of systematic turnover through geological time (Rothwell, 1996a). In the past few years, Paleozoic fossil ferns have been assigned to the Cladoxylales, Iridopteridales, Rhacophytales, Coenopteridales, and Stauropteridales (Taylor & Taylor, 1993), and extinct species have been described for all major groups with living representatives (Stewart & Rothwell, 1993).

Until recently, relationships of ferns above the family level have been frustratingly resistant to systematic resolution (Gifford & Foster, 1989; Smith, 1995). At least in part, this is because fern systematics traditionally has been interpreted using morphological data from living species only (Smith, 1995). Traditional studies have generally suffered from a perceived paucity of informative characters and from ineffective methodologies for the resolution of systematic relationships. As a result, dramatically different hypotheses of fern relationships have resulted from studies by the most respected authorities (e.g., Wagner, 1969, 1989; Bierhorst, 1971; Holttum, 1973; Mickel, 1974; Pichi Sermolli, 1977), and fossil taxa have played almost no role in formulating these hypotheses. Rather, extinct species either have been omitted from such studies or have been fitted into classifications devised from living species alone (e.g., Tidwell & Ash, 1994).

As the result of more than 150 years of paleobotanical investigations, we have developed an extensive record of well-known fossilized fern species (e.g., Collinson, 1996), a general understanding of the geological ranges for major fern groups (e.g., Cleal, 1993; Collinson, 1996; Rothwell, 1996a), and a sophisticated appreciation for the evolution of fern organs (e.g., Galtier & Phillips, 1996). Recent studies have also demonstrated that extinct species provide crucial data for cladistic studies (Gauthier et al., 1988; Donoghue et al., 1989; Rothwell & Serbet, 1994; Rothwell & Stockey, 1994), particularly for the resolution of deep nodes of phylogenetic trees and for developing an understanding of the overall phylogenetic pattern of ancient clades (Huelsenbeck, 1991).

Only recently have extinct species been incorporated into systematic studies for the simultaneous resolution of fern relationships (e.g., Skog, 1992; Rothwell, 1994, 1996a; Rothwell & Stockey, 1994) and have molecular characters become available for phylogenetic analysis. Nevertheless, analyses that include either extinct species or molecular data have already dramatically augmented, clarified, and/or altered classifications based on traditional interpretations of morphological data from living species alone (Crane, 1985; Stein et al., 1992; Hasebe et al., 1994; Rothwell & Stockey, 1994; Wolf et al., 1994; Conant et al., 1995; Crane et al., 1995; Gastony & Rollo, 1995; Hasebe et al., 1995; Haufler & Ranker, 1995; Hauk, 1995; Manhart, 1995; Pryer et al., 1995; Raubeson & Stein, 1995; Wolf, 1995). Moreover, results derived from each of the available data sources are serving as meaningful tests for hypotheses generated by studies using the others (c.f. Hasebe et al., 1994; Rothwell & Stockey, 1994; Pryer et al., 1995; Stevenson & Loconte, 1996).

The current study represents the first attempt to address global questions of fern phylogeny by numerical cladistic analysis using morphological characters of both extinct and living taxa and to resolve the overall phylogenetic pattern for plants that we recognize as ferns s.l. Questions explored in the study include: Are ferns s.l. monophyletic, or do they represent a paraphyletic or polyphyletic grade group? What are the relationships of ferns s.l. to other major groups of vascular plants? Are the psilotophytes (i.e., *Psilotum* and *Tmesipteris*) more closely related to early fossil land plants, as traditionally interpreted, or to filicalean ferns, as hypothesized by Bierhorst (1968, 1971, 1977)? Do the Ophioglossales represent ferns as traditionally interpreted, or are they derived from progymnosperms, as hypothesized by Bierhorst (1971) and others (e.g., Kato, 1988)? Some of these questions have been addressed previously, but never within a phylogenetic context that includes fossils.

## III. Nature of the Study

Basic relationships among land plants were recently analyzed in a comprehensive study that included both bryophytes and the most ancient extinct species of polysporangiophytes from uppermost Silurian and Devonian deposits (Kenrick & Crane, 1997). When combined with information from studies that include more recent tracheophyte taxa (Rothwell, 1995:

Fig. 1), these results provide a framework within which to explore the global relationships of ferns s.l. (Fig. 1).

Kenrick and Crane (1997: Fig. 4:31) recognize as the "Euphyllophytina" a clade that includes Devonian representatives of trimerophytes, equisetophytes, fernlike plants, and progymnosperms, and their analysis identifies six synapomorphies that define this clade (Fig. 1). These are: pseudomonopodial or monopodial branching; a basically helical arrangement of branches; small, "pinnulelike" vegetative branches (non-planate in basal taxa); recurvation of branch apices; sporangia in pairs grouped into terminal trusses; and multicellular appendages (spines). Their results arrange the Devonian species such that a clade consisting of the progymnosperm *Tetraxylopteris* plus the trimerophyte *Pertica* is the sister group to a clade that includes fernlike plants and the putative equisetophyte *Hyenia* (Kenrick & Crane, 1997: Fig. 4:31). However, when geologically more recent polysporangiophytes also are considered (e.g., Rothwell, 1994), relationships among ferns, equisetophytes, and lignophytes are equivocal (Rothwell, 1996b: Fig. 1).

The present investigation builds on the systematic background provided by these earlier studies to focus on the phylogenetic relationships of ferns. By necessity this constitutes a global analysis of relationships among taxa of the Euphyllophytina sensu Kenrick and Crane (1997). It includes some of the same taxa analyzed by Kenrick and Crane (i.e., *Aglaophyton* and *Psilophyton*), plus representatives from all of the monophyletic groups that are considered geologically more recent sister groups or descendants of the other taxa analyzed by these authors (Kenrick & Crane, 1997; Fig. 1; Appendix 1).

## IV. Methods

The current study includes 52 taxa that represent all of the major groups of ferns and fernlike plants (Rothwell, 1996a), as well as representatives of lignophytes, equisetophytes, and other putatively related groups that make up the Euphyllophytina (Kenrick & Crane, 1997; Appendix 1). Of the terminal taxa, 26 are extinct and 26 have living species. These include 13 extant homosporous filicaleans, 17 extinct homosporous and heterosporous ferns from Paleozoic strata, five extant and one extinct heterosporous leptosporangiate ferns, two extant marattiaceous ferns, two extant ophioglossaceous ferns, one extant and two extinct equisetophytes, both extant homosporous psilotophytes (i.e., *Psilotum* and *Tmesipteris*), one extinct heterosporous progymnosperm, three extinct and one extant seed plants, and the extinct homosporous trimerophyte *Psilophyton crenulatum* (Appendix 1). To root the tree, the basal rhyniophytoid polysporangiophyte, *Aglaophyton major* (Kenrick & Crane, 1997; Appendix 1), was also included in the analysis.

There is a tremendous disparity of completeness with which species of extinct plants have been reconstructed and are understood as organisms. Some fossil plant species are as well known as most species of living plants and can be scored for most of the characters used in this analysis. Other taxa, such as species of the Iridopteridales, are not fully enough characterized (Taylor & Taylor, 1993) to make meaningful contributions to the global resolution of fern relationships (Huelsenbeck, 1991; Nixon, 1996). Therefore, inclusion of such taxa is deferred until they can be reconstructed as plants and scored for a much larger percentage of the characters. Concepts for the extinct taxa included in the analyses are presented in Appendix 1.

The phylogenetic analyses employed 101 morphological characters (Appendix 2). The process of building a character matrix for psilotophytopsid polysporangiophytes has been ongoing for the past four years, with the number of characters and terminal taxa increasing

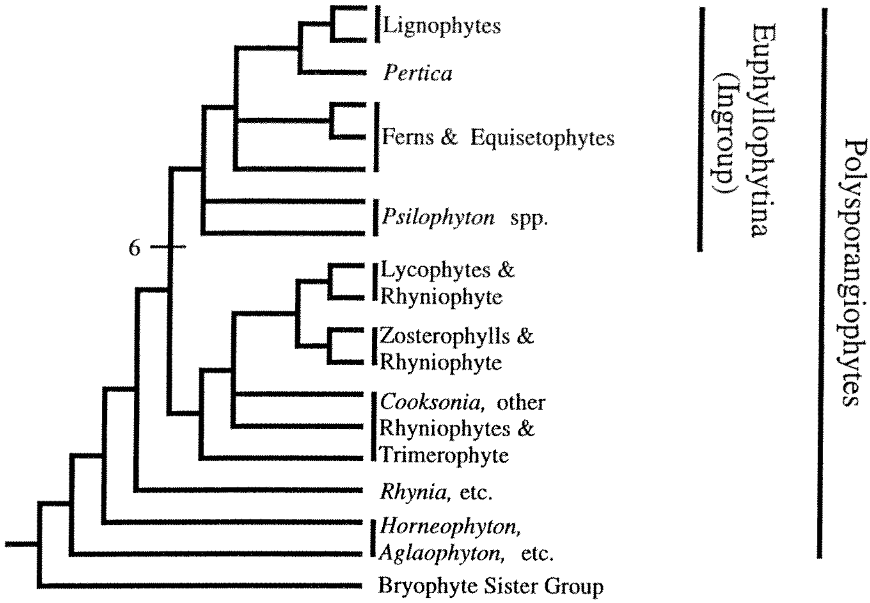


**Fig. 1.** Tree showing hypothesized relationships among polysporangiophytes, to identify the taxa to be included in the current analyses (i.e., the Euphyllophytina sensu Kenrick and Crane, 1997). Six synapomorphies that define this clade are detailed in the text. Modified from Fig. 4:31 of Kenrick and Crane (1997) with data from Fig. 1 in Rothwell (1995).

steadily throughout the period (e.g., Rothwell, 1994, 1996a). Many of the characters have been developed during this process; others have been adopted or modified from earlier analyses (see Smith, 1995) or are comparable to characters developed independently by other workers (e.g., Pryer et al., 1995). An explanation of the origins of each character is included in Appendix 2.

Relationships among all 52 taxa were resolved in unconstrained, simultaneous maximum parsimony analyses (Nixon & Carpenter, 1993) and rooted through *Aglaophyton*, the most basal polysporangiophyte (Kenrick & Crane, 1997). Of the 101 characters (Table I), 74 were binary, 18 were 3-state, four were 4-state, three were 5-state, one was 6-state, and one was 9-state (Appendix 2). Characters for which data were not available for some taxa and characters that were not applicable to some taxa were all scored as "?." Characters that were variable within a terminal taxon were scored for all of the appropriate states. Unequivocal character scoring ranged from 71% to 100% for all terminal taxa except *Hydropteris pinnata*, which could be scored for only 52% of the characters (Appendix 1). The mean of scored characters was 81.7% for extinct taxa, 97.9% for extant taxa, and 89.8% for all taxa.

The percentage of characters that could be scored unequivocally is included, with an explanation of the concept for each terminal taxon (Appendix 1). Because this percentage was relatively high for each taxon (i.e., more than 70% for all taxa except *Hydropteris*), it is unlikely that common scoring for equivocal and inapplicable characters significantly affected tree topology. Nevertheless, a test of this assumption was conducted (i.e., relationships were analyzed with *Hydropteris pinnata* omitted); the results are discussed below.

PAUP (version 3.1.1; Swofford, 1993), installed on a Macintosh PowerMac 7100 computer, was used to generate most parsimonious trees (heuristic search, one tree held at each step, TBR branch swapping, MULPARS). The analysis was replicated 1000 times using the "random addition" of taxa option of PAUP to increase the search space of possible cladograms. In addition, a two-step method for improving the probability that all islands of trees would be found (Maddison, 1991) was employed as described by Pryer et al. (1995). Decay analyses were conducted to provide measures of strength for phylogenetic hypotheses represented by tree topology. Additional analyses were conducted with some taxa omitted to provide comparative information about the effects of extinct species and missing characters on tree topology. MacClade (version 3.01; Maddison & Maddison, 1992) was used to plot character distributions onto the resultant topologies.

## V. Results

### A. TREE TOPOLOGY

The analysis yielded 12 most parsimonious trees of 429 steps with a consistency index (CI) of 0.35 and a retention index (RI) of 0.71. The most parsimonious trees are located in two islands of six trees each. The RI for these results (i.e., 0.71) is slightly higher than for any of the data matrices analyzed by Maddison (1991) that also had most parsimonious trees distributed in more than one island. The strict consensus tree of these 12 trees is fully resolved except for the occurrence of polytomies among filicalean ferns and a polytomy at one node among the seed plants (Fig. 2). These results suggest that ferns s.l. are polyphyletic, with fern-like plants occurring in three distantly related clades (Fig. 2).

There are five important clades in the consensus tree (Fig. 2). Progressing distally, these clades are: the stauropterid ferns (Fern Clade #1); the trimerophyte *Psilophyton crenulatum;* the living psilotophytes *Psilotum* + *Tmesipteris;* a clade consisting of the lignophytes + (equisetophytes + Paleozoic ferns of the Cladoxylales and Zygopteridales) (Fern Clade #2); and a clade that includes all of the fern groups with living species (Fern Clade #3).

In Fern Clade #1 the homosporous species *Stauropteris oldhamia* is sister to the heterosporous species *Gillespiea randolphensis* + *Stauropteris burntislandica*. *Cladoxylon* is sister to *Rhacophyton* plus the zygopterid ferns *Biscalitheca musata* + *Corynepteris involucrata* in Fern Clade #2. Fern Clade #3 consists of the eusporangiate ferns *Ophioglossum* + *Botrychium* (i.e., Ophioglossales) as sister group to the eusporangiate marattialean ferns plus the leptosporangiate ferns. Within the marattialean clade, the Paleozoic genus *Psaronius* is sister to the living genera *Marattia* + *Angiopteris.*

Leptosporangiate ferns are monophyletic and branch from several nodes at the top of the tree (Fig. 2). *Gleichenia* + *Stromatopteris* + *Hymenophyllum* form a polytomy that is most basal in the leptosporangiate clade. A polytomy at the next node consists of *Osmunda* + *Schizaea* + the Permian species *Skaaripteris minuta* + a clade that consists of several Carboniferous fossil taxa + a clade that includes the heterosporous Hydropteridales + several living genera of Filicales.

The hydropterid clade shows the marsileacous genera (*Marsilea* + (*Regnellidium* + *Pilularia*)) as sister group to *Hydropteris pinnata* + (*Salvinia* + *Azolla*). The filicalean genera *Matonia*, *Dennstaedtia*, *Adiantum*, and *Pteridium* occur in a pectinate arrangement at successively more distal nodes below a clade that consists of *Cyathea* + *Acrostichum* as sister group to *Onoclea* + *Polypodium*.

**Table I**

Character matrix[a]

| | 1 | 11 | 21 | 31 |
|---|---|---|---|---|
| *Aglaophyton major* | 0000000000 | 00000?0000 | ?000000000 | 0000000000 |
| *Psilophyton crenulatum* | 000?000000 | 00010?0000 | ?000000000 | 0000102100 |
| *Cladoxylon* | 000?101100 | 0000???000 | ?0??102200 | 000212?02 |
| *Rhacophyton* | 000?1011?? | 000010?202 | ?0?0000200 | 0000212100 |
| *Biscalitheca musata* | 000?000100 | 000010?202 | 3011100000 | 0000414100 |
| *Corynepteris involucrata* | 000?000100 | 000010?202 | 3011100000 | 0000414100 |
| *Stauropteris burntislandica* | 000??00??? | 0000???001 | ?000100100 | 0000202000 |
| *Stauropteris oldhamia* | 000??00??? | 0000???001 | ?000101100 | 0000202000 |
| *Gillespiea randolphensis* | 000??00??? | 0000???001 | ?000000100 | 0000202000 |
| *Psilotum* | 0000000020 | 00010?0000 | 0000001A00 | 0000B04100 |
| *Tmesipteris* | 0010000020 | 00010?0000 | 0000001100 | 0000204100 |
| *Psaronius* | 000?101110 | 000011?100 | 1011012000 | 1111302010 |
| *Marattia* | 0001101110 | 0000111100 | 1011012000 | 1111202012 |
| *Angiopteris* | 0001101110 | 0000111100 | 1011012000 | 1111202012 |
| *Botrychium* s.l. | 0000100110 | 0000100210 | C010002000 | 1100304100 |
| *Ophioglossum* | 0000100110 | 0000100210 | 011000200? | ??00304101 |
| *Ankyropteris brongniartii* | 000?110121 | 000010?100 | 1010000000 | 0000202000 |
| *Sermaya* plant | 000???0100 | 001010?100 | 1010000000 | ??00203100 |
| *Botryopteris forensis* | 001?100100 | 001010?100 | 1010000000 | 0000204100 |
| *Botryopteris cratis* | ??0?1001?? | 001010?100 | 1010000000 | 0000104100 |
| *Botryopteris tridentata* plant | 000?1001?0 | 001010?100 | 1010002000 | 1100304100 |
| *Psalixochlaena antiqua* | 000?0?0120 | 0010???100 | ?010000000 | 0000203000 |
| *Psalixochlaena cylindrica* | 000?000120 | 001010?100 | 1010000000 | 0000203000 |
| *Anachoropteris clavata* plant | 000?1201?0 | 001010?100 | 1010000000 | 0000404100 |
| *Skaaripteris minuta* | 000?000100 | 00?010???? | ???0002000 | 1100203000 |
| *Osmunda* | 0001100110 | 0000101100 | 1010002000 | 1010203100 |
| *Schizaea* | 0001100120 | 0000101100 | 2010002000 | 1100202100 |
| *Gleichenia* | 0001000100 | 0000101100 | 1011000000 | 1100202100 |
| *Stromatopteris* | 000?000120 | 0000100100 | 1011000000 | 1100C02000 |
| *Hymenophyllum* | 0001000120 | 0000101100 | 0010000000 | 1100D02100 |
| *Matonia* | 0001000100 | 0000100100 | 1110002000 | 110120??10 |
| *Cyathea* | 0001101110 | 0000101100 | 1011002000 | 1110202112 |
| *Dennstaedtia* | 0001000100 | 0010101100 | 1010002000 | 1100204110 |
| *Pteridium* | 0001000100 | 0010101100 | 1011002000 | 1110204112 |
| *Acrostichum* | 0001100110 | 0000101100 | 1111002000 | 1110203112 |
| *Adiantum* | 0001C00120 | 0000101100 | 1001002000 | 110020??11 |
| *Onoclea* | 0001000120 | 0000100100 | 1111002000 | 1110204111 |
| *Polypodium* | 0001000100 | 0000101100 | 1011002000 | 111020??12 |
| *Marsilea* | 1001000100 | 0000100100 | 1110002000 | 1100204110 |
| *Pilularia* | 1001000100 | 0000100100 | 1010002000 | 1100202110 |
| *Regnellidium* | 1001000100 | 0000100100 | 1010002000 | 1100202110 |
| *Hydropteris pinnata* | 100?000100 | ?0001??100 | 111000???? | ?????????? |
| *Salvinia* | 1101000100 | 00000??100 | 0110000000 | 0000?02100 |
| *Azolla* | 1101000100 | 0000101100 | 0010000000 | 0000?02100 |
| *Equisetum* | 1000000121 | 0100101100 | 0000002010 | 0000203100 |
| *Calamites* | 100?001121 | 010010?100 | 0000002010 | 000020B100 |
| *Archaeocalamites* | 100?000121 | 010010?100 | ?000002010 | 0000204100 |
| *Archaeopteris* | 000?101100 | 000010?100 | ?0?0002001 | 0000204100 |
| *Elkinsia polymorpha* | 000?1001?? | ??00???100 | ?0?0000201 | 0000204101 |
| *Lyginopteris oldhamia* | 000?100121 | 100010?100 | 1010002001 | 0000204101 |
| *Medullosa* | 000?111121 | 100010?100 | 1010002001 | 0000204102 |
| *Pinus* | 0002101121 | 1000101100 | 0000002001 | 0000304101 |

[a] Key: A = 0/1/2; B = 2/4; C = 0/1; D = 1/2; E = 1/3.

| 41 | 51 | 61 | 71 | 81 | 91 |
|---|---|---|---|---|---|
| 0000000000 | 0000000?00 | 0000000000 | 000000?0?0 | 000000?000 | ??000000?? |
| 0000100000 | 0000000000 | 0000000000 | 000000?0?0 | 000000?000 | ??????0??? |
| 0000102001 | 1000010000 | 0000000000 | 000000???0 | 000?0????? | ??????0??? |
| 010013?001 | 100?012000 | 0000000000 | 000000?0?0 | 000000?110 | 00????0??? |
| 2100132001 | 10?1011002 | 1000100000 | 10010420?0 | 000000?0?0 | ??????0??? |
| 2100132001 | 10?1011002 | 1000100000 | 10010320?0 | 000000?0?0 | ??????0??? |
| 1000240000 | 00000?0000 | 0000000000 | 000000?0?1 | ?10000?1?0 | ?0????0??? |
| 1000240000 | 00000?0000 | 0000000000 | 000000?0?0 | 000000?1?0 | ?0????0??? |
| 1000240000 | 00000?0000 | 00000?0000 | 100000???1 | ?1000????? | ?0????0??? |
| 1000243100 | 0010012002 | 0110110000 | 100000?000 | 0000010010 | 0010000000 |
| 0000240000 | 0010012002 | 0110110000 | 100000?000 | 0000010010 | 0010000000 |
| 2002210110 | 000?010002 | 1000110000 | 000000?0?0 | 00000C?010 | 00????0??? |
| 2002110000 | 0000010002 | 1000110000 | 000000?000 | 0000010010 | 0070100100 |
| 2002110000 | 0000010002 | 10001?0000 | 000000?000 | 0000000010 | 0070100101 |
| 2002211001 | 100001200D | 1000000000 | 000000?000 | 0000000010 | 002010000C |
| 2002211000 | 0000012001 | 0000000000 | 000000?000 | 0000000010 | 0020100000 |
| 2000230000 | 0000010002 | 1000100000 | 10110201?0 | 000000?0?0 | ?0????0??? |
| 2001210000 | 0000010002 | 1000100000 | 00110201?0 | 000000?1?0 | ?0????0??? |
| 2010210000 | 0000012000 | 0000000000 | 101100?1?0 | 0000001000 | ?0????0??? |
| 2010210000 | 00?0012000 | 0000000000 | 10110101?0 | 0000001010 | 00????0??? |
| 2010210000 | 0000011002 | 1000100001 | 10110101?0 | 000000?0?0 | ?0????0??? |
| 2000210000 | 000001000D | 1000100000 | 10110101?0 | 000000?0?0 | ?0????0??? |
| 2001210000 | 000001000D | 1000100000 | 10110101?0 | 000000?0?0 | ?0????0??? |
| 2001210000 | 0000010002 | 1000101110 | 2111051l?0 | 000000?0?0 | ?0????0??? |
| 2012210100 | 000001?001 | 1000100000 | 1011020??0 | 000000?0?0 | ?0????0??? |
| 2002212100 | 0010112001 | 0000000000 | 10C1020110 | 0000000010 | 0070000?10 |
| 2012212101 | 0010012002 | 1000000001 | 1011120110 | 0000011010 | 0031010100 |
| 2012210000 | 0010010002 | 1000100000 | 1011151110 | 00000C0110 | 0070000??0 |
| 2002210000 | 0010110001 | 0000101000 | 1011151110 | 0000010010 | 0020000??? |
| 2002210000 | 0010010001 | 0000101110 | 1011121110 | 0000000010 | 0041100110 |
| 0002210110 | 0000110002 | 1000100010 | 10111E1220 | 0000000120 | 1061000110 |
| 2002242110 | 0010110002 | 1000101110 | 2011111210 | 0000001110 | 00600101?0 |
| 2002210100 | 0000110001 | 0000100110 | 2011112220 | 0000001120 | 0061010110 |
| 2002240010 | 0010110001 | 0000101210 | 2111112220 | 0000001120 | 1061010110 |
| 2002242000 | 0010111002 | 1000101200 | 2111112220 | 0000001120 | 0061010110 |
| 2002211100 | 0000110001 | 0000101201 | 2011112220 | 0000001120 | 2061010110 |
| 2002210000 | 0010012002 | 1000101111 | 2111112220 | 0000011120 | 0061010110 |
| 2002240000 | 0010010002 | 1000101200 | 2111112220 | 0000011010 | 0061010110 |
| 2002210100 | 0010012102 | 1000100110 | 101000?211 | 1100001120 | 0081210110 |
| 2002210100 | 0010012102 | 1000100110 | 101000?211 | 1100001120 | 1081210110 |
| 2002210100 | 0010012102 | 1000100110 | 101000?211 | 1100001120 | 1081210110 |
| ?????????? | 00???12102 | 100010???0 | ??1??0?2?1 | ?100001120 | 21??2?0??? |
| 2000211000 | 0010012111 | 0000101010 | 101000?211 | 1100001120 | 2181210110 |
| 0000211000 | 0010012111 | 0000101010 | 101000?211 | 1100001120 | 21812101C0 |
| 0000102000 | 0010012002 | 0001001000 | 000000?100 | 0000021111 | 0050000000 |
| 0000102001 | 1011012002 | 0001001000 | 000000?10C | ??0000?111 | 00????0??? |
| 0000102001 | 1011012002 | 0001001000 | 000000?1?0 | 000000?1?? | 00????0??? |
| 0000100001 | 1101011002 | 010010?000 | 000000?2?1 | ?00000?100 | ?0????0??? |
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| 2002103001 | 110101D002 | 0000110000 | 000000?2?1 | 111010?100 | ?0822?11?? |
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| 0000211001 | 1101012002 | 1000100000 | 000000?201 | 1111110100 | ?082221121 |

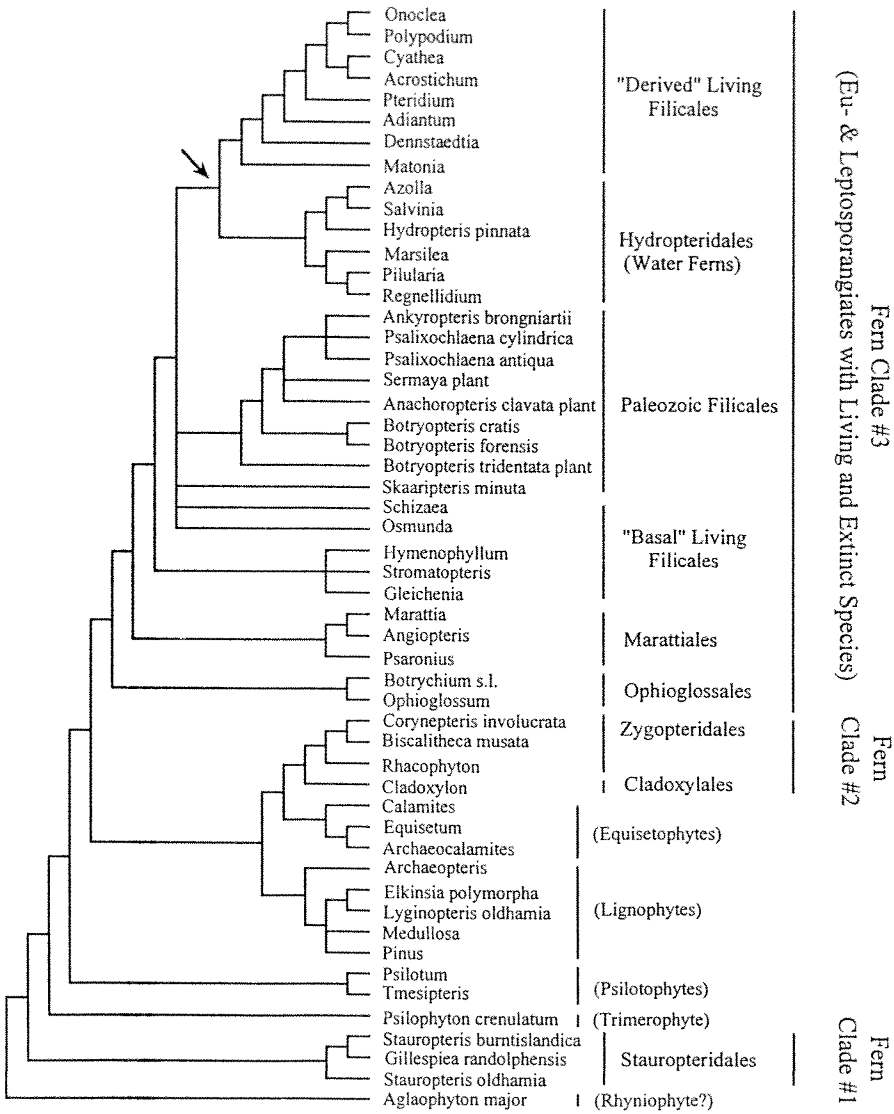


**Fig. 2.** Strict consensus of 12 most parsimonious trees of 429 steps found in the results of the complete analysis. Three clades of ferns are recognized, and terminal taxa are identified with regard to the group or groups of plants that they represent. Decay index values are indicated for several clades of interest. The arrow indicates the position of the hydropterid node.

## B. DECAY ANALYSIS

To test the relative strengths of nodes on the strict consensus tree of the 12 most parsimonious trees, a decay analysis was conducted. There are 852 trees of 430 steps, one step longer than the most parsimonious tree, and there are 23,259 trees of 431 steps. Due to the treesaving limitations of the software, the number of successively longer trees and the number of steps required to reduce the Euphyllophytina to a polytomy could not be determined. Nodes of the strict consensus tree that decay at two steps longer than the most parsimonious trees and at three or more steps longer than the most parsimonious trees are indicated in Figure 2. Clades that decay at three or more steps include stauropterid ferns, psilotophytes, zygopterid ferns (of Fern Clade #2), marattialean ferns, Fern Clade #1, and hydropterid ferns.

### C. CHARACTER CHANGES ON REPRESENTATIVE TREE

To understand those synapomorphies that characterize several clades identified in the results, the number of unambiguous character changes on the branch below each clade of interest was plotted on a representative tree arbitrarily chosen from among the 12 most parsimonious trees of 429 steps (Fig. 3). Clades of interest include stauropterid ferns (Fern Clade #1), cladoxylopsid ferns plus *Rhacophyton* + zygopteridalean ferns (Fern Clade #2), and eusporangiate plus leptosporangiate ferns with living and extinct representatives (Fern Clade #3), ophioglossalean ferns, marattialean ferns, and leptosporangiate ferns (i.e., filicalean plus hydropteridalean ferns).

#### *1. Stauropterid Ferns*

There are five character-state changes on the branch leading to the stauropterid ferns (Fern Clade #1 in Fig. 3). These changes are: #20, quadriseriate branching of axes/leaves absent → throughout; #28, stele with radiating arms of xylem absent → as rounded lobes; #41, radial axis/rachis trace round-elliptical → lobed; #46, position of protoxylem in rachis/axis toward no face → toward several faces; and #88, exospore surface nearly smooth or plain → obviously sculptured.

#### *2. Fern Clade #2*

A single character state changes on the branch subtending Fern Clade #2, sister group to the equisetophytes (Fig. 3): #36, peripheral loops absent → present. Progressing distally within Fern Clade #2 are four character-state changes on the branch that subtends *Rhacophyton* + (*Biscalitheca* + *Corynepteris*). These are: #20, quadriseriate branching of axes/leaves absent → at base only; #27, pith in stem/axis above base → absent; #42, clepsydroid petiole trace absent → present; and #46, position of protoxylem in rachis/axis toward no face → lateral).

Eleven character states change on the branch subtending *Biscalitheca* + *Corynepteris*: #5, growth form of stem/axis erect → rhizomatous; #7, arborescence present → absent; #24, scales absent → present; #35, protoxylem of stem/axis mesarch → exarch; #41, radial rachis/axis trace round-elliptical → absent; #57, meio/microsporangium bearing structure unlike vegetative → somewhat modified from the vegetative; #61, abaxially attached sporangia absent → present; #65, meio/microsporangial grouping absent → present; #71, sporangial stalk absent → broad; #74, functional annulus absent → present; and #88, exospore surface nearly smooth or plain → obviously sculptured.

#### *3. Fern Clade #3, with Living and Extinct Representatives*

There are five character-state changes on the stem of the tree subtending the node that represents the common ancestor of Fern Clade #3 (Fig. 3). These are: #31, stele with leaf gaps in

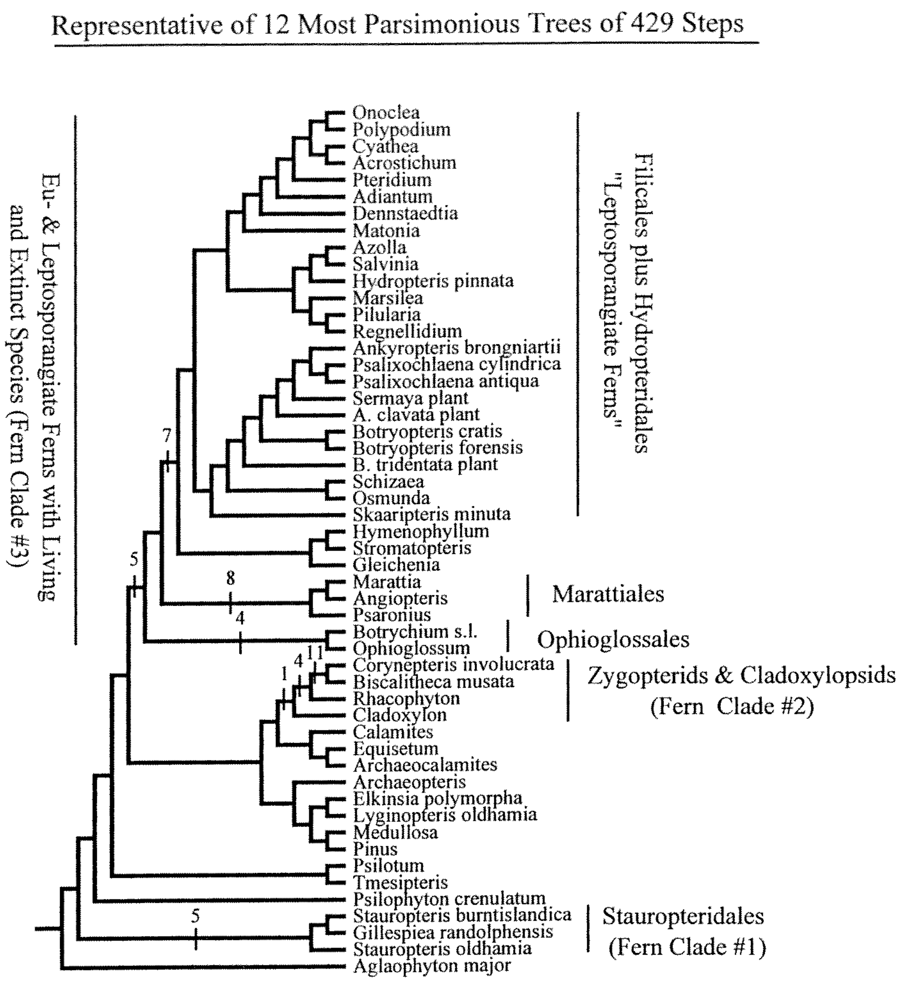


**Fig. 3.** Representative of the 12 most parsimonious trees of 429 steps found in the results of the complete analysis. Major groups of ferns are identified, and the number of character changes that occur on several branches of the tree are indicated. See the text for the identities of character changes.

xylem absent → present; #32, stele with leaf gaps in phloem absent → present; #41, radial rachis/axis trace round-elliptical → absent; #44, "C" shaped trace absent → adaxially convex; and #46, position of protoxylem in rachis/axis toward no face → adaxial.

## *4. Ophioglossalean Ferns*

Four character states change on the branch subtending the ophioglossalean ferns (Fig. 3). These are: #18, planation of vegetative leaves throughout → in distal regions only; #19, basal division of trophophore absent → present; #35, protoxylem of stem/axis mesarch → exarch; and #47, sclerenchyma in cortex as continuous cylinder → absent.

### *5. Marattialean Ferns*

Eight character-state changes occur on the branch leading to the marattialean ferns (Fig. 3). These are: #7, arborescence absent → present; #16, root anatomy 2–5 arch → polyarch; #26, stipules absent → present; #33, dictyostele absent → present; #34, polycyclic stele absent → present; #38, borders on metaxylem pitting present → absent; #39, phloem disposition ectophloic → amphiphloic; and #66, sporangia fused forming synangia absent → present.

### *6. Leptosporangiate Ferns*

On the branch leading to the group that traditionally has been referred to as leptosporangiate ferns are seven character-state changes (Fig. 3). These are: #5, growth form of stem/axis erect → rhizomatous; #71, sporangial stalk absent → broad; #73, sporangial capsule large with thick wall → small with thin wall; #74, functional annulus absent → present; #78, number of spores per meio/microsporangium >512 → 128–512; #79, ontogenetic origin of sporangia from several cells → from approximately two cells; and #99, first division of zygote more or less transverse → more or less longitudinal.

## D. TAXON OMISSION EXPERIMENTS

### *1.* Hydropteris

Only 52% of the characters could be scored for *Hydropteris pinnata* (Table I). This was dramatically lower than the mean for the analysis as a whole (89.8%), far lower than the mean for all other extinct taxa (81.7%), and considerably lower than for the next lowest value (71%, for *Gillespiea randolphensis*). To test the hypothesis that the degree of resolution obtained in the results may have been artificially improved due to a relaxation of global parsimony resulting from this relatively large percentage of equivocal character scoring (Nixon, 1996), the analysis was reinitiated with *H. pinnata* omitted. This analysis yielded 12 most parsimonious trees of 428 steps that were identical to those for the complete analysis except that they were one step shorter and that *H. pinnata* was absent. The consistency and retention indices were the same as for the complete analysis (CI = 0.35; RI = 0.71). These results suggest that the inclusion of *H. pinnata* did not artificially increase the degree of resolution illustrated by the strict consensus tree (Fig. 2).

### *2. Extinct Taxa*

For comparison with results of previous studies by other authors that included living taxa only, an analysis was conducted with all of the extinct terminal taxa except *Psilophyton crenulatum* omitted from the character matrix. *Psilophyton crenulatum* was included for the purpose of rooting the tree. This "extant-only" analysis included the 26 extant taxa with living representatives (Appendix 1). Due to the exclusion of the extinct taxa, only 81 of the characters in the original matrix (Table I, Appendix 2) were phylogenetically informative. The uninformative characters (numbers 3, 6, 11, 12, 20, 25, 28, 29, 30, 36, 42, 52, 54, 56, 64, 83, 84, 85, 90, and 97) were omitted from the analysis.

This analysis yielded one most parsimonious tree of 279 steps (Fig. 4), with consistency and retention indices of 0.42 and 0.67, respectively. Progressing distally from the root, *Psilo-*

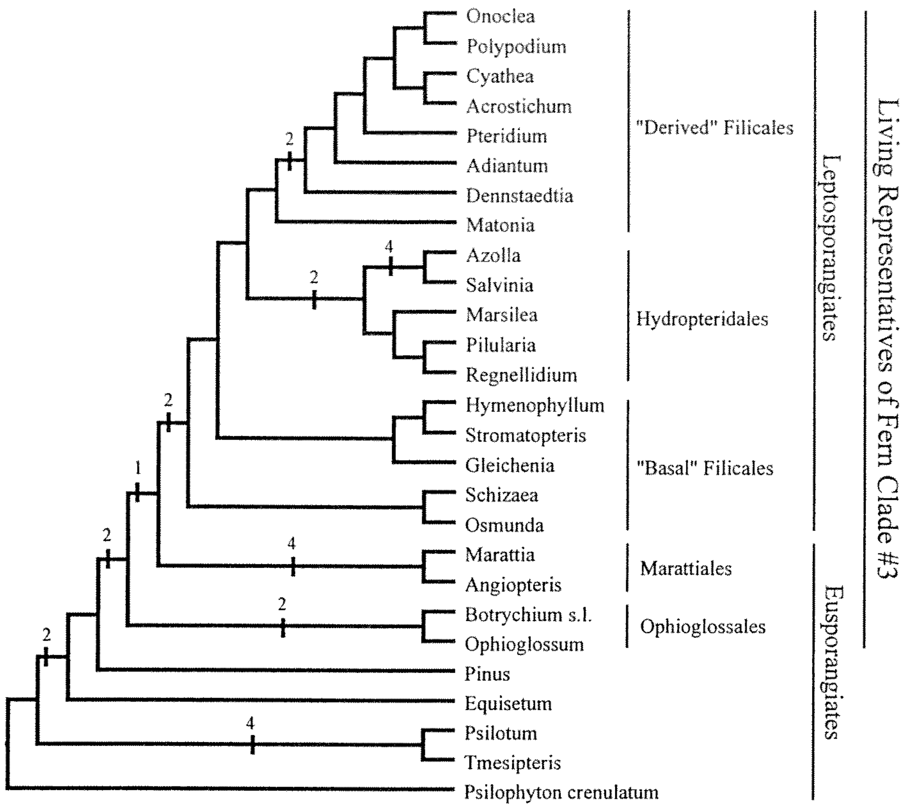


**Fig. 4.** One most parsimonious tree of 279 steps found in the results of the "extant only" analysis. Decay index values are indicated for several clades of interest.

*phyton crenulatum*, the most basal clade, comprises the psilotophytes *Psilotum* + *Tmesipteris*, followed by the equisetophyte *Equisetum*, the seed plant *Pinus*, the ophioglossalean ferns *Ophioglossum* + *Botrychium*, the marattiaceous ferns *Marattia* + *Angiopteris*, and the "leptosporangiate" clade that consists of the Filicales + the Hydropteridales (Fig. 4).

As in the complete analysis, the "leptosporangiate" clade is monophyletic and includes a paraphyletic Filicales and a monophyletic Hydropteridales (Fig. 4). This clade consists of a paraphyletic group of "basal Filicales," with the Hydropteridales + the "derived Filicales" as sister groups at the apex of the tree (Fig. 4). Among the filicales, *Osmunda* + *Schizaea* form the most basal clade, with *Gleichenia* + (*Stromatopteris* + *Hymenophyllum*) attached to the stem at the next node (Fig. 4). Topology of the Hydropteridales is exactly as in the complete analysis, except that the fossil species *H. pinnata* is absent. The clade of "derived" Filicales is resolved in the same way as in the complete analysis (cf. Figs. 2 & 4).

Although more completely resolved at the base than comparable regions of the consensus tree for the complete analysis (Fig. 2), decay index values suggest that the nodes in the "basal" Filicales and "derived" Filicales regions of the "extant only" tree are not strongly supported (Fig. 4).

## VI. Comparison with Traditional Interpretations and with Results of Analyses by Other Authors

### A. PSILOTUM AND TMESIPTERIS

The psilotophytoid genera *Psilotum* and *Tmesipteris* traditionally were interpreted as relatively unaltered descendants of the most primitive vascular plants. However, a fossil record to document this relationship was absent (e.g., Andrews, 1961). In the late 1960s Bierhorst drew attention to morphological and anatomical similarities between the psilotophytes and the gleichenioid filicalean, *Stromatopteris*, and hypothesized that *Psilotum* and *Tmesipteris* were most closely related to this genus (Bierhorst, 1968, 1971, 1977).

Results of the analyses reported here support the hypothesis that *Psilotum* + *Tmesipteris* form a monophyletic group, with this clade near the base of the euphyllophyte tree (sensu Kenrick & Crane, 1997). In the complete analysis the psilotophytes occur at a node below the position where the clade consisting of lignophytes + (Fern Clade #2 + Equiseopthytes) is attached (Figs. 2 & 3), and in the "extant only" analysis they are the most basal clade (Fig. 4). Therefore, filicalean affinities for these extant genera are not supported by the results presented here. These results compare favorably with those from the "extant only" analysis of morphological characters by Stevenson and Loconte (1996), in which the psilotophytes clade is attached to the stem at a node above the Lycopodiales and below the Equisetales (Stevenson & Loconte, 1996: Fig. 1).

### B. OPHIOGLOSSALES AND MARATTIALES

Results of both the complete analysis (Fig. 2) and the "extant only" analysis (Fig. 4) support the Ophioglossales as a monophyletic group. Arrangement of Ophioglossales as sister group to Marattiales plus leptosporangiates in the results of both analyses (Figs. 2 & 4) supports traditional systematic interpretations for the living ferns (e.g., Gifford & Foster, 1989). Analyses using molecular characters (i.e., *rbc*L gene sequencing) also place the eusporangiate ferns at the base of the tree that includes the leptosporangiates. However, the arrangement of the eusporangiates and additional sister groups varies both among and within the molecular analyses (Hasebe et al., 1994, 1995; Pryer et al., 1996). Representatives of the Marattiales are basal in some, but in others, representatives of Ophioglossales and Marattiales either form a small clade or are members of an unresolved polytomy at the base of the tree.

On the other hand, results obtained here (Figs. 2 & 4) do not support the alternative hypothesis that Ophioglossales is derived from the progymnosperms, such as *Archaeopteris* (e.g., Bierhorst, 1971; Kato, 1988). Rather, nesting of the Ophioglossales within living ferns as the basal taxon of this monophyletic group (Fern Clade #3 in Figs. 2–4) suggests that ophioglossaleans are accurately recognized as ferns.

Results of the complete analysis, in which marattialean ferns form a monophyletic group with the Paleozoic genus *Psaronius* sister to the extant genera *Marattia* + *Angiopteris*, also conform to expectations based on traditional interpretations (Gifford & Foster, 1989; Stewart & Rothwell, 1993; Taylor & Taylor, 1993). These results are roughly concordant with those of an earlier and more thorough cladistic analysis of marattialean ferns (Hill & Camus, 1986). Likewise, placement of Marattiales in the current results (Figs. 2 & 4) as sister group to the leptosporangiate Filicales + Hydropteridales agrees with traditional systematic interpretations (Gifford & Foster, 1989).

## C. LEPTOSPORANGIATE FERNS

Traditional classifications of leptosporangiate ferns recognized several families of apparently primitive filicaleans ("basal" filicaleans in this analysis), two or more families of more highly derived Filicales ("derived" filicaleans in this analysis), and two groups of heterosporous water ferns (Gifford & Foster, 1989). Both Bower (1923–1928) and Copeland (1947) recognized the Osmundaceae, Schizaeaceae, Hymenophyllaceae, Gleicheniaceae, Matoniaceae, and possibly Cyatheaceae as relatively primitive ("basal") filicaleans and the Marsileaceae and Salviniaceae as distinct, distantly related families of heterosporous ferns. A majority of leptosporangiate diversity was encompassed by the apparently more highly derived species that Bower (1923–1928) included in the Polypodiaceae and Dicksoniaceae and that Copeland (1947) and more recent authors have recognized as a variable number of distinct families (Pteridaceae, Davalliaceae, Aspleniaceae, Aspidiaceae, Blechnaceae, Polypodiaceae, etc.; Bierhorst, 1971; Holttum, 1973; Mickel, 1974; Pichi Sermolli, 1977; Wagner, 1989; Kramer, 1990).

In the results of the current study, the Paleozoic filicalean taxa (not included in previous analyses) occur among the "basal" filicaleans (Fig. 2). However, in the current results this is the least resolved region of the tree (Fig. 2), and there are several apparently novel arrangements of extant filicalean taxa (Figs. 4 & 5). Note particularly that a clade consisting of *Gleichenia* + *Hymenophyllum* + *Stromatopteris* is basal among the leptosporangiates, that *Matonia* is attached above (rather than below) the hydropterid node, and that *Cyathea* occurs at the top of the tree (rather than either just below or just above the hydropterid node, as in previous analyses; Stein et al., 1992; Hasebe et al., 1994, 1995; Rothwell & Stockey, 1994; Pryer et al., 1995; Stevenson & Loconte, 1996).

Topology of the hydropterid clade conforms precisely to the results of most previously published analyses of morphological (Rothwell & Stockey, 1994; Pryer et al., 1995) and molecular characters (Hasebe et al., 1995), except that the fossil taxon *Hydropteris* was excluded from some. In the results of a living-species-only analysis of morphological characters by Stevenson and Loconte (1996) the positions of *Marsilea* and *Pilularia* are reversed from the results of the other analyses.

The recent discovery that heterosporous leptosporangiate ferns (i.e., Hydropteridales in Figs. 2–4) form a monophyletic group nested within the filicaleans (Hasebe et al., 1994, 1995; Rothwell & Stockey, 1994; Pryer et al., 1995; Stevenson & Loconte, 1996) provides a benchmark for resolving relationships within the leptosporangiate clade. Results of earlier analyses using morphological and/or molecular data (Stein et al., 1992; Hasebe et al., 1994, 1995; Rothwell & Stockey, 1994; Wolf et al., 1994; Pryer et al., 1995; Stevenson & Loconte, 1996) are roughly concordant with those presented here. The monophyletic Hydropteridales occurs as sister group to the derived Filicales (Figs. 2 & 4) at a node in the midregion of the leptosporangiate tree. Results of these studies are also concordant with respect to the remaining filicaleans (i.e., Basal Filicales in Fig. 4), which occur as a paraphyletic assemblage of clades attached to the stem of the tree below this "hydropterid node" (the arrow in Figs. 2 & 4).

The basal filicalean families recognized from the results presented here (Figs. 2 & 4) are more or less concordant with the "primitive" families of traditional classifications (Bower, 1923–1928; Copeland, 1947; Gifford & Foster, 1989) and also with the filicalean taxa attached to the stem below the "hydropterid node" (the arrow in Figs. 2 & 4) in the results of both molecular and morphological/molecular analyses by other authors (Hasebe et al., 1994, 1995; Pryer et al., 1995; Stevenson & Loconte, 1996; Fig. 5). However, beyond these general

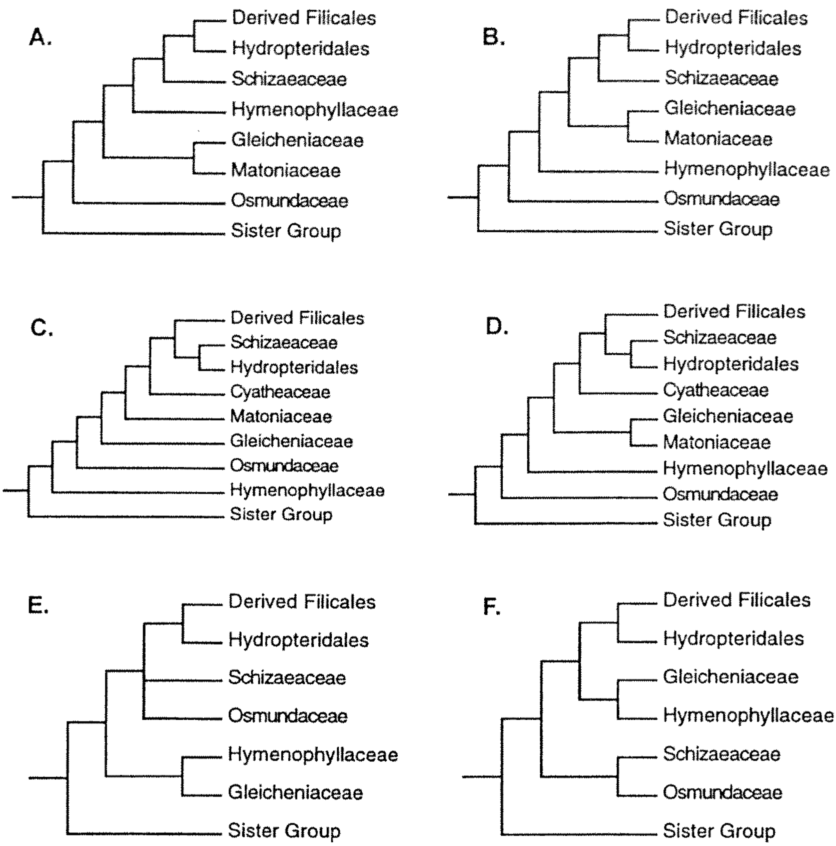


**Fig. 5.** Trees showing variations among recent phylogenetic hypotheses for the relationships among Leptosporangiate fern families. Only families attached at and below the hydropterid node (see Fig. 2) are identified. **A.** Simplified from results of equal weighted maximum parsimony analysis of *rbc*L by Hasebe et al. (1995: Fig. 3). **B.** Simplified from results of neighbor joining analysis of *rbc*L by Hasebe et al. (1995: Fig. 1). **C.** Simplified from results of combined morphology and *rbc*L analysis by Pryer et al. (1995: Fig. 11). **D.** Simplified from results of morphological analysis of characters from living species only by Stevenson and Loconte (1996: Fig. 4). **E.** Simplified from results of the complete analysis of morphological characters of living and extinct taxa (Fig. 2). **F.** Simplified from results of the living species only analysis of morphological characters (Fig. 4). See the text for details.

similarities, results of recent phylogenetic analyses vary considerably (Fig. 5). Osmundaceae is the basal leptosporangiate clade in the results of most studies (Figs. 5A, 5B, 5D, & 5F), but Hymenophyllaceae is basal in the combined *rbc*L/morphological results of Pryer et al. (1995; Fig. 5C), and Hymenophyllaceae + Gleicheniaceae is basal in the results of the combined extant/extinct analysis presented here (Fig. 5E). Schizaeaceae is either attached to the stem of the tree immediately below the hydropterid node (Figs. 5A, 5B, & 5E) or is sister group to Hydropteridales (Figs. 5C & 5D), except in the results of the extant-only analysis presented here (Fig. 5F). Cyatheaceae occurs below the hydropterid node in the results of Pryer et al. (1995;

Fig. 5C) and of Stevenson and Loconte (1996: Fig. 5D) and above this node (i.e., among the derived filicales) in the results of the other analyses (Fig. 5).

Although there is a growing consensus that leptosporangiate ferns form a clade in which the monophyletic Hydropteridales is embedded within the paraphyletic Filicales, the disparity of results from recent phylogenetic analyses (Fig. 5) emphasizes that familial circumscriptions and relationships among filicalean families remain incompletely resolved. This is particularly evident for basal filicalean families that reflect the most ancient cladogenic events within the leptosporangiate clade.

Paleontology is providing crucial data for resolving the deepest internal branches of the vascular plant tree and for developing a hypothesis of overall relationships among ferns s.l. We anticipate that future analyses which combine morphological data from living and fossil species will prove equally valuable for resolving familial relationships among families of homosporous leptosporangiate ferns.

## VII. Summary


1. Ferns s.l. are a polyphyletic grade group that resolves as three clades nested within the Euphyllophytina sensu Kenrick and Crane (1997).

2. Stauropterid ferns are attached to the stem of the euphyllophyte tree near the base. Therefore, stauropterids are the most distantly related clade of plants that has traditionally been interpreted as ferns (i.e., Fern Clade #1 in Fig. 2).

3. The psilotophytes *Psilotum* and *Tmesipteris* form a small clade that is also attached to the stem near the base of the tree. Therefore, this clade resolves as most closely related to extinct primitive land plants, as asserted in traditional morphological and paleobotanical interpretations. The hypothesis that *Psilotum* and *Tmesipteris* are closely related to the Filicales (Bierhorst, 1968, 1971, 1977) is not supported by the results of the current analyses.

4. Cladoxylalean ferns plus Zygopteridalean ferns (including *Rhacophyton*; Fern Clade #2 in Fig. 2) form a clade that is related more closely to equisetophytes and lignophytes than to other groups of fernlike plants. This indicates that the sporangial annulus has evolved separately in zygopterid and filicalean ferns.

5. Eusporangiate and Leptosporangiate fern groups with living representatives form a monophyletic group (Fern Clade #3 in Fig. 2). This is in agreement both with traditional morphological systematics (e.g., Gifford & Foster, 1989) and with the results of cladistic analyses by other authors using both morphological and molecular characters (Hasebe et al., 1994, 1995; Pryer et al., 1995; Stevenson & Loconte, 1996).

6. Ophioglossales is a monophyletic group that forms the sister group to all other taxa of Fern Clade #3.

7. The Marattiales is also monophyletic and is the nearest sister group to the "leptosporangiate" ferns.

8. The "leptosporangiate" ferns form a clade that includes the Filicales plus the Hydropteridales.

9. Within the "leptosporangiate" clade the Hydropteridales is monophyletic and is nested within the Filicales, which is a paraphyletic grade group.

10. Filicales consist of a basal assemblage and a derived clade that forms the sister group to the Hydropteridales. The basal filicalean clade includes several families with living representatives as well as the Paleozoic species that traditionally were considered to be coenopterid ferns (e.g., Eggert, 1964).

11. Relationships among the filicalean families are not adequately resolved.

## VIII. Acknowledgments

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## Appendix 1: Taxa Included in the Study

Concepts for the taxa used in this study were developed from a large number of sources. Twenty-six of the taxa have living representatives, and data for character scoring of these taxa is largely available in the literature. Particularly helpful information for the scoring of such characters is presented by Bierhorst (1971), Bower (1923–1928), Eames (1936), Ogura (1972), Tryon and Lugardon (1990), and Tryon and Tryon (1982). Numerous additional sources for character scorings were compiled by Pryer et al. (1996). Concepts for nine of the extinct taxa are based on plant reconstructions that have been conducted by the author and several collaborators (*Gillespiea randolphensis*, *Medullosa*, *Elkinsia polymorpha*, *Biscalitheca musata*, *Corynepteris involucrata*, *Botryopteris tridentata* plant, *Botryopteris forensis*, *Anachoropteris clavata* plant, and *Hydropteris pinnata*). Concepts for four additional extinct taxa were modified to varying degrees from previously published reports (*Skaaripteris minuta*, *Sermaya* plant, *Psalixochlaena antiqua*, and *Psalixochlaena cylindrica*). These modifications are explained in the appropriate places in Appendixes 1 and 2. Concepts for 12 other extinct species were taken directly from the literature (*Aglaophyton major*, *Stauropteris oldhamia*, *Stauropteris burntislandica*, *Psilophyton crenulatum*, *Lyginopteris oldhamia*, *Archaeopteris*, *Archaeocalamites*, *Calamites*, *Cladoxylon*, *Rhacophyton*, *Psaronius*, and *Botryopteris cratis*).

## CONCEPTS FOR TAXA INCLUDED IN THE STUDY

*Aglaophyton major* (89% of characters scored). Based on reconstruction of the sporophyte phase by Edwards (1986) and of the gametophyte phase as summarized by Remy et al. (1993). Additional data from Remy and Hass (1996).

*Psilophyton crenulatum* (84% of characters scored). Based on the reconstruction by Dorn (1980).

*Cladoxylon* (73% of characters scored). Based largely on *C. scoparium,* as described by Kräusel and Weyland (1926) and by Schweitzer and Giesen (1980). See the summary by Taylor and Taylor (1993).

*Rhacophyton* (81% of characters scored). Based on the reconstruction of *R. ceratangium* by Andrews and Phillips (1968) and augmented by data from other studies (Leclercq, 1951, 1954; Cornet et al., 1976; Dittrich et al., 1983).

*Biscalitheca musata* (84% of characters scored). Based on reconstructions of vegetative features (Dennis, 1974) and reproductive structures (Millay & Rothwell, 1983) and on ongoing reconstructions of Upper Pennsylvanian zygopterid ferns from North American coal balls (Rothwell, 1988; Trivett & Rothwell, unpubl. data).

*Corynepteris involucrata* (84% of characters scored). Based on reconstructions of vegetative features (Dennis, 1974) and reproductive structures (Trivett, 1986) and on ongoing reconstructions of Upper Pennsylvanian zygopterid ferns from North American coal balls (Rothwell, 1988; Trivett & Rothwell, in prep.).

*Stauropteris burntislandica* (76% of characters scored). Based on data presented by Bertrand (1909), Surange (1952a), and Chaloner (1958), summarized by Taylor and Taylor (1993).

*Stauropteris oldhamia* (77% of characters scored). Based on data from Binney (1872) and Eggert (1964), summarized by Taylor and Taylor (1993).

*Gillespiea randolphensis* (71% of characters scored). Based on the reconstruction by Erwin and Rothwell (1989).

*Psilotum* (96% of characters scored). Based on living species. See particularly Bierhorst (1971).

*Tmesipteris* (98% of characters scored). Based on living species. See particularly Bierhorst (1968, 1971).

*Psaronius* (85% of characters scored). Composite concept based on reconstructions of vegetative and fertile structures by Morgan (1959), Stidd (1971), and Millay (1979, 1982).

*Marattia* (99% of characters scored). Based on living species.

*Angiopteris* (98% of characters scored). Based on living species.

*Botrychium* s.l. (95% of characters scored). Based on living species.

*Ophioglossum* (96% of characters scored). Based on living species.

*Ankyropteris brongniartii* (88% of characters scored). Based on the reconstruction by Mickle (1980) and references cited therein.

*Sermaya* plant (83% of characters scored). Composite concept, based on vegetative structures of the Anachoropteridaceae (Phillips, 1974) and on fertile structures described by Eggert and Delevoryas (1967). Although this is a composite concept, all of the parts co-occur at two separate sources, and few characters are ambiguous among the probable alternatives for the correct organs of the plant.

*Botryopteris forensis* (88% of characters scored). Based on the reconstruction by Rothwell (1991), with data derived from references cited therein.

*Botryopteris cratis* (84% of characters scored). Based on data presented by Millay and Taylor (1980) and Phillips (1974).

*Botryopteris tridentata* plant (85% of characters scored). Based on previously developed data summarized by Phillips (1974) and on an ongoing reconstruction of the plant from coal balls collected near West Mineral, Kansas (Good & Rothwell, 1991).

*Psalixochlaena antiqua* (82% of characters scored). Based on data presented by Surange (1952b), Holden (1962), and Galtier (1967, 1981) and following the systematic revision of Good (1981).

*Psalixochlaena cylindrica* (85% of characters scored). Based on the reconstruction by Holmes (1977, 1981), augmented by data from Good (1981). Following the work of Good (1981), sporangial maturation within a sorus is interpreted as simultaneous rather than gradate, as interpreted earlier (Holmes, 1981).

*Anachoropteris clavata* plant (85% of characters scored). Based on data presented by Delevoryas and Morgan (1954), Rothwell (1987), and Trivett and Rothwell (1988) as part of an ongoing reconstruction of the plant (Rothwell, unpubl. data).

*Skaaripteris minuta* (77% of characters scored). Based on data presented by Galtier and Taylor (1994), with some alterations of interpretation. The divergence of a leaf trace in *S. minuta* produces a discontinuity in the stelar cylinder. However, the discontinuity is closed by convergence of vascular tissue from each side of the gap at a lower level than that at which the trace separates from the stele. This was originally interpreted as a leaf gap not being produced (Galtier & Taylor, 1994). However, because divergence of a leaf trace creates a continuity between the ground tissue of the pith and cortex, *S. minuta* is interpreted here as producing an extremely low leaf gap. In this analysis the character is scored as leaf gap present.

*Osmunda* (98% of characters scored). Based primarily on living species.

*Schizaea* (99% of characters scored). Based on living species.

*Gleichenia* (96% of characters scored). Based on living species.

*Stromatopteris* (95% of characters scored). Based on living species.

*Hymenophyllum* (98% of characters scored). Based on living species.

*Matonia* (97% of characters scored). Based on living species.

*Cyathea* (98% of characters scored). Based on living species.

*Dennstaedtia* (100% of characters scored). Based on living species.

*Pteridium* (100% of characters scored). Based on living species.

*Acrostichum* (100% of characters scored). Based on living species.

*Adiantum* (97% of characters scored). Based on living species.

*Onoclea* (100% of characters scored). Based on living species.

*Polypodium* (98% of characters scored). Based on living species.

*Marsilea* (99% of characters scored). Based on living species.

*Pilularia* (99% of characters scored). Based on living species.

*Regnellidium* (99% of characters scored). Based on living species.

*Hydropteris pinnata* (52% of characters scored). Based on the reconstruction presented by Rothwell and Stockey (1994).

*Salvinia* (96% of characters scored). Based on living species.

*Azolla* (97% of characters scored). Based on living species.

*Equisetum* (99% of characters scored). Based on living species.

*Calamites* (84% of characters scored). Based on the traditional concept (Stewart & Rothwell, 1993), as augmented by Good (1975). This is a composite concept for what undoubtedly is a large number of species.

*Archaeocalamites* (84% of characters scored). Based on the concept developed for this genus by Bateman (1991).

*Archaeopteris* (82% of characters scored). Comparable to the concept of Archaeopteridales of Rothwell and Serbet (1994), with characters scored as described by Beck and Wight (1988).

*Elkinsia polymorpha* (82% of characters scored). Comparable to the concept of Elkinsiales (Serbet & Rothwell, 1994), as scored by Rothwell and Serbet (1994).

*Lyginopteris oldhamia* (89% of characters scored). Comparable to the concept of *Lyginopteris* as defined by Rothwell and Serbet (1994).

*Medullosa* (89% of characters scored). Comparable to the concept of *Medullosa* as defined by Rothwell and Serbet (1994), with particular reference to the features of *M. endocentrica* sensu Hamer and Rothwell (1988).

*Pinus* (98% of characters scored). Based on living species.

## Appendix 2: Characters Used in the Analyses

1. Growth habit: 0 = terrestrial; 1 = amphibious or aquatic. [Modified from character 1 of Rothwell and Stockey, 1994; similar to character 36 of Pryer et al., 1995.]
2. Growth as floating aquatic: 0 = absent; 1 = present. [Modified from character 1 of Rothwell and Stockey, 1994; similar to character 36 of Pryer et al., 1995.]
3. Epiphytic growth: 0 = absent; 1 = present. [Segregated from character 36 of Pryer et al., 1995.]
4. Model of growth: 0 = psilotioid; 1 = selaginelloid; 2 = cotyledonoid. [New character, derived from the classification of growth models presented in Rothwell, 1995; somewhat similar to concept of character 72 of Pryer et al., 1995.]
5. Growth form of stem/axis: 0 = rhizomatous; 1 = erect. [Derived from character 17 of Hill and Camus (1986) and similar to character 26 of Pryer et al. (1995).]
6. Growth as a liana: 0 = absent; 1 = present. [New character.]
7. Arborescence: 0 = absent; 1 = present. [New character. Some plants grow upright by producing a stem that elongates to elevate the crown above the ground cover and to form the trunk of a tree. This character reflects growth form and is not necessarily correlated either with systematic relationships or with the production of secondary tissues.]
8. Clearly differentiated stem/leaf-shoot organography: 0 = absent; 1 = present. [New character. Sporophytes of the most ancient polysporangiophytes did not have stem/leaf organography of the shoot system. The independent evolution of leaves within several clades has led to the almost universal occurrence of the derived state among living vascular plants. *Psilotum* and *Tmesipteris* are interpreted by some authors (e.g., Bierhorst, 1968, 1971, 1977) to have rhizomes from which three-dimensional fronds are produced. However, the aerial systems of these plants do not arise from the basal systems in a definite arrangement, and they are not substantially differentiated from the basal axes in either branching pattern or internal anatomy. Therefore, the vegetative organs of the psilotophytes are interpreted to be homologous to the systems of axes and enations that also characterize extinct trimerophytes.]
9. Branching of stem/axis: 0 = apparently apical only; 1 = typically absent; 2 = lateral and/or from buds. [Modified from characters 1 and 2 of Doyle and Donoghue (1992), character 1 of Rothwell and Serbet (1994), and similar to excluded character 91 of Pryer et al. (1995).]
10. Branching consistently associated with nodes: 0 = absent; 1 = present. [Modified from characters 1 and 2 of Doyle and Donoghue (1992) and character 1 of Rothwell and Serbet (1994). Lang (1913) identified dormant axillary buds in *Botrychium*, but the stems usu-

ally are unbranched. See Holmes (1977, 1989) for discussion of various types of branch ing, including lateral branching that is not associated with nodes.]

11. Branches vascularized by two bundles that are derived from cauline bundles that flank th orthostichy of the subtending leaf: 0 = absent; 1 = present. [New character, derived fror Rothwell (1976).]
12. Branches alternating with leaves at nodes: 0 = absent; 1 = present. [New character.]
13. Epiphyllous branching: 0 = absent; 1 = present. [Similar to character 22 of Pryer et a (1995).]
14. Unvascularized enations: 0 = absent; 1 = present. [New character.]
15. Roots: 0 = absent; 1 = present. [Modified from character 2 of Rothwell and Stocke (1994), and comparable to character 33 of Pryer et al. (1995).]
16. Root anatomy: 0 = 2–5 arch; 1 = polyarch. [Derived from character 35 of Pryer et al (1995).]
17. Root hairs: 0 = absent; 1 = present. [Derived from character 35 of Pryer et al. (1995).]
18. Planation of vegetative leaves: 0 = absent; 1 = throughout; 2 = in distal region only. [Nev character, reflecting variations in frond architecture among ferns s.l.]
19. Biseriate vegetative leaves: 0 = absent; 1 = throughout; 2 = above basal fork; 3 = in dista regions only. [New character, reflecting the distinctive ontogeny/morphology of the fo liar organs in the Ophioglossales (Bierhorst, 1971).]
20. Quadriseriate branching of vegetative leaves: 0 = absent; 1 = throughout; 2 = at base only [New character, reflecting distinctive branching architecture found in some extinct fern (Stewart & Rothwell, 1993).]
21. Vernation: 0 = erect; 1 = adaxially rolled crosiers; 2 = abaxially rolled crosiers; 3 = erec rachis, abaxially rolled crosiers on primary pinnae, and adaxially rolled crosiers on mor distal frond segments. [Most plants that have circinate vernation of the leaves produc crosiers that roll toward the adaxial surface of the frond. In the case of axes with circinat tips, this is equivalent to rolling toward the subtending fork. However, in a few plants th fronds roll toward the abaxial surface of the frond, and in the zygopterid ferns *Biscalithe-cea* and *Corynepteris* frond ontogeny is more complex. In the latter genera the rachis ha erect vernation (Dennis, 1974), the primary pinnae roll toward the abaxial surface, an more distal pinnae are adaxially coiled (Trivett & Rothwell, unpubl. data). Related t concept of character 1 of Pryer et al. (1995).]
22. Venation of pinnule or ultimate axis: 0 = not anastomosing; 1 = anastomosing. [Derive from character 45 of Hill and Camus (1986) and similar to character 5 of Rothwell an Stockey (1994) and to character 7 of Pryer et al. (1995).]
23. Trichomes: 0 = largely absent; 1 = present. [Derived from character 44 of Hill and Camus (1986) and similar to characters 10 and 31 of Pryer et al. (1995).]
24. Scales: 0 = absent; 1 = present. [Similar to characters 11 and 31 of Pryer et al. (1995).]
25. Vascularized aphlebiae: 0 = absent; 1 = present. [New character, derived from features of zygopterid anatomy (e.g., Dennis, 1974).]
26. Stipules: 0 = absent; 1 = present. [Derived from character 5 of Hill and Camus (1986) and comparable to excluded character 89 of Pryer et al. (1995).]
27. Pith in stem/axis: 0 = absent; 1 = present. [New character, from traditional systematics.]
28. Stele with radiating arms of xylem: 0 = absent; 1 = as rounded lobes; 2 = as narrow ribs.]
29. Equisetostele: 0 = absent; 1 = present. [New character, from traditional systematics. The elaborate stelar architecture of *Equisetum* and of extant species of the Calamitales is unlike that of any other vascular plant (Bierhorst, 1971). Nevertheless, such steles have been variously termed "eusteles," or "solenosteles of the *Equisetum* type," and so forth

(Schmid, 1982). In this paper the term "equisetostele" is used to identify this distinct architecture.]

30. Stele with sympodial architecture: 0 = absent; 1 = present. [Modified from character 11 of Doyle and Donoghue (1992) and character 16 of Rothwell and Serbet (1994).]
31. Stele with leaf gaps in xylem: 0 = absent; 1 = present. [New character, somewhat comparable to the concept of character 27 of Pryer et al. (1995).]
32. Stele with leaf gaps in phloem: 0 = absent; 1 = present. [New character. The occurrence of leaf gaps traditionally has been interpreted from the configuration of the xylem, with the implicit assumption that the phloem conforms to the same configuration. However, this is not always the case. For the purpose of this analysis the presence of leaf gaps in the xylem and in the phloem has been separated into two characters, and *Osmunda* is distinguished from other terminal taxa with leaf gaps in the xylem (Hewitson, 1962).]
33. Dictyostele: 0 = absent; 1 = present. [Derived from character 1 of Hill and Camus (1986) and character 27 of Pryer et al. (1995).]
34. Polycyclic stele: 0 = absent; 1 = present. [Comparable to character 28 of Pryer et al. (1995).]
35. Protoxylem of stem/axis: 0 = none; 1 = centrarch; 2 = mesarch; 3 = endarch; 4 = exarch. [Modified from character 12 of Doyle and Donoghue (1992) and character 15 of Rothwell and Serbet (1994), and comparable to excluded character 92 of Pryer et al (1995).]
36. Peripheral loops: 0 = absent; 1 = present. [New character, from traditional paleobotanical systematics (e.g., Dennis, 1974).]
37. Pitting pattern of metaxylem: 0 = none; 1 = annular-helical; 2 = scalariform; 3 = multiseriate scalariform; 4 = oval-circular. [Modified from character 14 of Doyle and Donoghue (1992) and character 18 of Rothwell and Serbet (1994), and somewhat comparable to the concepts of character 25 and excluded character 93 of Pryer et al. (1995).]
38. Borders on metaxylem pitting: 0 = absent; 1 = present. [Somewhat comparable to the concept of excluded character 93 of Pryer et al. (1995). However, a much larger percentage of taxa used in the present analysis can be scored for this character.]
39. Phloem disposition: 0 = ectophloic; 1 = amphiphloic. [New character, from traditional systematics.]
40. Xylem at base of rachis/axis: 0 = single bundle; 1 = two bundles; 2 = numerous bundles. [Similar to character 23 of Pryer et al. (1995).]
41. Radial rachis/axis trace: 0 = round-elliptical; 1 = lobed; 2 = absent. [Comparable to character 23 of Pryer et al. (1995).]
42. Clepsadroid petiole trace: 0 = absent; 1 = present. [New character, from zygopterid fern studies (e.g., Galtier & Scott, 1985). Plants with rachis traces of this type show 180° rotational symmetry (Rothwell, 1986), with the plane of symmetry parallel to the periphery of the stem or axis.]
43. Omega-shaped trace: 0 = absent; 1 = present. [New character, based on anatomical studies of Paleozoic ferns. This trace configuration is well known for ferns assigned to the Carboniferous filicalean genus *Botryopteris* (Taylor & Taylor, 1993), but it also occurs in other ferns (Eames, 1936; Bierhorst, 1971; Good & Rothwell, 1988; Galtier & Taylor, 1994).]
44. "C"-shaped trace: 0 = absent; 1 = abaxially convex; 2 = adaxially convex. [From traditional systematics of Paleozoic species previously assigned to the Coenopteridales (e.g., Eggert, 1964). Both characters 43 and 44 are extensions of the morphological diversity displayed by the vascular tissues of frond rachides and are encompassed by character 24 of Pryer et al. 1995).]

45. Rachis/axis protoxylem between levels of branching: 0 = absent; 1 = internal; 2 = nea peripheral-peripheral. [New character. The protoxylem in leaf traces is surrounded b considerable metaxylem in some plants but is either at the periphery or nearly at the pe riphery in others. This character varies independently from the protoxylem/metaxlen disposition in the stem.]
46. Position of protoxylem in rachis/axis: 0 = toward no face; 1 = adaxial; 2 = abaxial; 3 = lat eral; 4 = toward several faces. [New character. Whereas character 45 reflects difference in maturation patterns of the xylem in fronds, this character reflects the position of pro toxylem with respect to the cross-sectional symmetry of the petiolar xylem.]
47. Cortical sclerenchyma: 0 = as continuous cylinder; 1 = absent; 2 = as scattered nests o bundles; 3 = as discontinuous cylinder. [Related to character 21 of Pryer et al. (1995).]
48. Pith sclerenchyma: 0 = absent; 1 = present. [Segregated from character 21 of Pryer et al (1995).]
49. Sclerenchyma accompanying vascular tissue of stele: 0 = absent; 1 = present. [From tradi tional systematics (e.g., Morgan, 1959) and related to character 21 of Pryer et al. (1996).]
50. Radially aligned tracheids: 0 = absent; 2 = present. [Essentially new character, separate from the concept of secondary xylem that has been produced by a cambium. However radial alignment of cells results from other developmental processes as well (e.g., Esau 1943; DeMason, 1983) and is not always correlated with the occurrence of either a unifacial or a bifacial vascular cambium (Cichan & Taylor, 1990; Rothwell & Pryor, 1991; Rothwell & Karrfalt, 1996). Related to concepts of characters 29 and 82 of Pryer et al. (1995).]
51. Xylem rays: 0 = absent; 1 = present. [Essentially new character, separated from the concept of secondary xylem and related to character 29 of Pryer et al. (1995). Not all plants that produce radially aligned secondary xylary elements also produce rays. See the explanation of character 50.]
52. Bifacial vascular cambium: 0 = absent; 1 = present. [Derived from "omitted" character 4 of Rothwell and Serbet (1994). Related to concept of characters 29 and 82 of Pryer et al. (1995).]
53. Endodermis in adult stem or axis: 0 = absent; 1 = present. [New character, from traditional systematics (e.g., Eames, 1936).]
54. Secondary cortex or periderm: 0 = absent; 1 = present. [New character.]
55. Adaxial outline of stipe/axis: 0 = convex or flattened; 1 = sulcate. [Derived from character 19 of Pryer et al. (1995).]
56. Sporangium produced by axis: 0 = present; 2 = absent. [New character, from traditional paleobotanical studies (Stewart & Rothwell, 1993).]
57. Meio/microsporangium-bearing structure: 0 = similar to vegetative; 1 = somewhat modified from vegetative; 2 = unlike vegetative. [Modified from character 47 of Hill and Camus (1986), and character 2 of Pryer et al. (1995).]
58. Sporocarps: 0 = absent; 1 = present. [Modified from character 9 of Rothwell and Stockey (1994) and character 2 of Pryer et al. (1995).]
59. Monosporangiate sporocarp: 0 = absent; 1 = present. [New character, from traditional systematics.]
60. Position of attachment of meio- or microsporangium: 0 = terminal; 1 = marginal; 2 = surficial. [Modified from character 28 of Rothwell and Serbet (1994) and related to character 49 of Pryer et al. (1995).]
61. Abaxially attached sporangia: 0 = absent; 1 = present. [Segregated from character 28 of Rothwell and Serbet (1994) and related to character 49 of Pryer et al. (1995).]

62. Adaxially attached sporangia: 0 = absent; 1 = present. [Segregated from character 28 of Rothwell and Serbet (1994) and related to character 49 of Pryer et al. (1995).]
63. Sporangia borne on forked enations: 0 = absent; 1 = present. [New character, from traditional systematics. This character recognizes the unique sporangial position found in *Psilotum* and *Tmesipteris*.]
64. Sporangia borne on sporangiophores: 0 = absent; 1 = present. [New character, from traditional systematics. This character recognizes that the sporangium-bearing structures of the equisetophytes are not homologous to sporophylls of other clades (Stewart & Rothwell, 1993).]
65. Meio/microsporangial grouping: 0 = absent; 1 = present. [Derived from character 7 of Rothwell and Stockey (1994) and comparable to character 47 of Pryer et al. (1995).]
66. Sporangia fused forming synangia: 0 = absent; 1 = present. [Modified from character 26 of Doyle and Donoghue (1992) and from character 33 of Rothwell and Serbet (1994) and comparable to character 83 of Pryer et al. (1995).]
67. Number of meio/microsporangia per group: 0 = few (usually <12); 1 = many (usually >20). [Comparable to character 51 of Pryer et al. (1995).]
68. Pattern of sporangial maturation: 0 = simple; 1 = gradate; 2 = mixed. [Comparable to character 50 of Pryer et al. (1995).]
69. Indusium: 0 = absent; 1 = present. [Segregated from character 6 of Rothwell and Stockey (1994) and the same as character 52 of Pryer et al. (1995).]
70. Sporangia enclosed by abaxially rolled lamina, forming a false indusium: 0 = absent; 1 = present. [Segregated from character 6 of Rothwell and Stockey (1994).]
71. Sporangial stalk: 0 = absent; 1 = broad; 2 = narrow. [Similar to character 45 of Pryer et al. (1995).]
72. Length of sporangial stalk: 0 = sessile-short; 1 = long. [The same as character 44 of Pryer et al. (1995).]
73. Sporangial capsule: 0 = large with thick wall; 1 = small with thin wall. [Related to character 42 of Pryer et al. (1995). This character is usually associated with either eu- or leptosporangiate development of the sporangium, but sporangial development falls into more than two types among ferns (see character 79). Therefore, mature capsule structure is an inaccurate predictor of sporangial development.]
74. Functional annulus: 0 = absent; 1 = present. [Fern capsules display a rich suite of characters that have been defined in a variety of ways. Characters 74–78 of this analysis segregate several capsule characters that show dissimilar distributions among the terminal taxa. An alternative approach to the segregation of capsule characters is reflected by characters 56–58 of Pryer et al. (1995).]
75. Uniseriate annulus: 0 = absent; 1 = present. [This reflects the distinction between the uniseriate annulus of most living filicaleans and the bi- or multiseriate annulus that occurs in Paleozoic filicaleans and the Osmundaceae (Good, 1979; Good & Rothwell, 1988). See the explanation of character 74.]
76. Annular ring: 0 = diffuse; 1 = wide lateral opening; 2 = narrow lateral opening; 3 = narrow basal opening; 4 = open apically and basally; 5 = narrow apical opening. [See the explanation of character 74.]
77. Orientation of annulus: 0 = absent or unoriented; 1 = horizontal; 2 = oblique; 3 = longitudinal. [See the explanation of character 74. Related to character 57 and to excluded character 98 of Pryer et al. (1995), but the less variable structure found among the terminal taxa used in this analysis has allowed for the scoring of most of the taxa.]

78. Number of spores per meio/microsporangium: 0 = >512; 1 = 128–512; 2 = <128. [Comparable to character 46 of Pryer et al. (1996).]
79. Ontogenetic origin of sporangia: 0 = from several cells; 1 = from approximately two cells; 2 = from one cell. [New character. Sporangial ontogeny among ferns ranges from eusporangiate to leptosporangiate, with a relatively large number of filicaleans being intermediate (i.e., sporangia derived from approximately 2 cells). This character reflects the gradation by recognizing three states.]
80. Sexual reproduction: 0 = homosporous; 1 = heterosporous. [Derived from character 8 of Rothwell and Stockey (1994) and comparable to character 59 of Pryer et al. (1995).]
81. Coenocytic development of megagametophyte: 0 = absent; 1 = present. [New character, from traditional systematics.]
82. One or two megaspores only: 0 = absent; 1 = present. [Modified from character 9.3 of Crane (1985) and character 2 of Rothwell and Serbet (1994). This character reflects the origin of "extreme heterospory" as a modification of the heterosporous life cycle (Rothwell, 1996b).]
83. Meio/megasporangial dehiscence: 0 = present; 1 = absent. [Modified from character 29 of Doyle and Donoghue (1992) and character 35 of Rothwell and Serbet (1994).]
84. Nonhydrasperman pollen chamber: 0 = absent; 1 = present. [Modified from character 42 of Rothwell and Serbet (1994).]
85. Integument with micropyle: 0 = absent; 1 = present. [Modified from character 36 of Rothwell and Serbet (1994).]
86. Meio/microspore morphology: 0 = radial and trilete; 1 = bilateral and monolete; 2 = radial and alete. [Derived from character 70 of Hill and Camus (1986) and related to character 60 and to excluded character 100 of Pryer et al. (1995).]
87. Exospore structure: 0 = 2-layered; 1 = 3-layered. [Modified from character 12 of Rothwell and Stockey (1994) and comparable to character 65 of Pryer et al. (1995).]
88. Exospore surface: 0 = nearly smooth or plain; 1 = obviously sculptured. [Character derived from Tryon and Lugardon (1990) and similar to characters 70–73 of Hill and Camus (1986) and to character 65 of Pryer et al. (1995).]
89. Perispore of meio/microspore: 0 = absent; 1 = thin, conforming to contours of exine; 2 = thick, forming contours of spore wall. [Modified from character 13 of Rothwell and Stockey (1994) and related to the concepts of characters 63, 64, and 84 of Pryer et al. (1995).]
90. Perispore forming elaters: 0 = absent; 1 = present. [New character, from traditional systematics (Stewart & Rothwell, 1993).]
91. Fine structure of meio/microspore perispore: 0 = solid; 1 = filamentous; 2 = lamellar. [Derived from character 14 of Rothwell and Stockey (1994).]
92. Meio/microsporangiate massulae: 0 = absent; 1 = present. [Modified from character 11 of Rothwell and Stockey (1994).]
93. Form of mature prothallus: 0 = highly branched and vascularized; 1 = subterranean, elongate, and cylindrical; 2 = tuberous and subterranean; 3 = filamentous; 4 = branched and ribbon shaped; 5 = deeply lobed; 6 = cordate, may be branched; 7 = cordate, becoming ribbon like; 8 = highly reduced. [Modified from character 68 of Pryer et al. (1995).]
94. Prothallus: 0 = thick or with midrib; 1 = thin, without midrib; 2 = alveolar. [Segregated from character 68 of Pryer et al. (1995).]
95. Position of antheridia: 0 = surficial; 1 = embedded. [Modified from character 73 of Pryer et al. (1995).]

96. Morphology of antheridia: 0 = large, several irregular jacket cells; 1 = small, few regularly arranged jacket cells; 2 = without jacket. [Modified from character 75 of Pryer et al. (1995).]
97. Pollination preceding fertilization: 0 = absent; 1 = present. [New character, reflecting synapomorphy of spermatophytes (Stewart & Rothwell, 1993).]
98. Potential number of sporophytes per prothallus: 0 = two or more; 1 = one. [New character, derived from life-cycle variations among embryophytes (Rothwell, 1995).]
99. First division of zygote: 0 = more or less transverse; 1 = more or less longitudinal; 2 = free nuclear. [Modified from character 41 of Pryer et al. (1995).]
100. Suspensor: 0 = present; 1 = absent. [New character, from traditional systematics.]
101. Aboveground organs of sporophyte from: 0 = apical hemisphere of proembryo; 1 = basal hemisphere of proembryo; 2 = lateral hemisphere of proembryo. [Comparable to character 41 of Pryer et al. (1995).]

**Note:** A phylogenetic analysis of relationships among living pteridophytes appeared while revision of this article was being completed (Stevenson & Loconte, 1996). The character definitions and character scorings of Stevenson and Loconte (1996) have not yet been critically evaluated in relation to those of this study.

**Correction! Please note:**

The sentence in the descriptor for Fig. 2 “Decay index values are indicated for several clades of interest” belongs with the descriptor for Fig. 3.